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RESEARCH ARTICLE

River embankments mitigate the loss of grassland biodiversity in agricultural landscapes

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Abstract

Agricultural intensification has resulted in severe declines in the extent and diversity of seminatural habitats in Europe, whereas the extent of secondary habitats has increased considerably. River embankments have become one of the most extensive and widespread secondary habitats in former floodplains. We compared the diversity patterns of secondary dry and wet grasslands on river embankments with those of seminatural dry and wet grasslands in a Hungarian agricultural landscape using the following community descriptors: (a) species diversity, (b) phylogenetic diversity and (c) functional diversity. We also performed trait-based analyses to evaluate the ecosystem services provided by these secondary grasslands. Both grassland types of the embankments showed significantly higher Shannon diversity compared with their seminatural counterparts. The cover of generalist species (i.e., cosmopolitan species, weeds and nonindigenous plant species) was high in the secondary grasslands. We found significant differences in phylogenetic diversity between the secondary and seminatural grasslands: secondary grasslands showed significantly lower mean nearest taxon distances than the seminatural grasslands. Functional diversity did not differ between the secondary and seminatural grasslands according to the Rao's quadratic entropy. However, we found higher community-weighted means of specific leaf area, plant height and flowering period in the secondary grasslands, which are related to important ecosystem services (via biomass production and pollination). Well-planned management actions and restoration activities could help further improve the ecological function and conservation value of secondary grasslands on river embankments, contributing to the maintenance of species diversity and sustaining the functionality of ecosystems in agricultural landscapes.

KEYWORDS

ecosystem services, functional diversity, functional traits, phylogenetic diversity, secondary grasslands

Zoltán Bátori and Péter János Kiss contributed equally to this study.

1 | INTRODUCTION

Technological advances in the second half of the 20th century have resulted in unprecedentedly rapid agricultural intensification worldwide (Baessler & Klotz, 2006), leading to a global-scale decline of the species and habitat diversity of ecosystems (Benton, Vickery, & Wilson, 2003). Landscapes with a high proportion of natural grasslands have largely been converted into arable fields, built-up areas and forest plantations (Bastian & Bernhardt, 1993; Biró, Bölöni, & Molnár, 2018). For instance, a large proportion of loess grasslands in Europe have been ploughed for cereal production because of their fertile chernozem soils (Deák et al., 2018; Erdős et al., 2018). Today, this grassland type mainly occurs in small fragments (e.g., on ancient burial mounds, earthen fortifications, road verges or at the margins of arable fields) and its area is still shrinking (Deák et al., 2016; Molnár, Biró, Bartha, & Fekete, 2012). The area and diversity of the European wet grasslands have also significantly declined in the last 300 years due to inappropriate management, drainage and river regulation (Maltby & Blackwell, 2005; Timmermann, Margóczi, Takács, & Vegelin, 2006). Along regulated rivers, wet grasslands can usually be found in the narrow and frequently disturbed (i.e., periodically flooded) floodplains between the river and the embankments (Varga, Dévai, & Tóthmérész, 2013).

A number of studies suggest that secondary habitats can act as refuges for native, endangered or vulnerable species, thus they may play key roles in the maintenance of biodiversity in transformed landscapes (e.g., in agricultural landscapes and settlements; Hobbs, Higgs, & Harris, 2009). For instance, city walls may provide valuable habitats for ferns (Láníková & Lososová, 2009), highway stormwater ponds for aquatic macroinvertebrates (Le Viol, Mocq, Julliard, & Kerbiriou, 2009), graveyards for orchids (Löki, Deák, Lukács, & Molnár, 2019; Molnár et al., 2017), kurgans (i.e., burial mounds) for steppe species (Deák et al., 2016), roadside verges for endangered lizard-orchids (Fekete et al., 2017) and plantation forests for vulnerable plant species (Bátori et al., 2020; Süveges et al., 2019). Further studies show that linear anthropogenic structures (e.g., ditches, hedgerows, river embankments and road verges) have the potential to form dispersal corridors not only for the native biota but also for many invasive species (Corbit, Marks, & Gardescu, 1999; Fekete, Mesterházy, Valkó, & Molnár, 2018; Francis, Chadwick, & Turbelin, 2019). Grasslands on embankments can be used as pastures or hay meadows and provide suitable habitats for pollinators (cf. Liebrand & Sykora, 1996). Although the area of secondary grasslands on river embankments is more than 15,000 ha in Hungary, data on their ecological function and conservation value are scarce (but see Bátori et al., 2016; Sallai, Harcsa, Szemán, & Percze, 2011; Torma & Császár, 2013).

The precise assessment of the ecological function and conservation value of different habitats is not possible based only on species diversity measures, because these methods neglect the functional complementarity and redundancy of species (Díaz & Cabido, 2001; Schleuter, Daufresne, Massol, & Argillier, 2010) and some of the information provided by more complex analysis of species is lost (Cadotte, Cavender-Bares, Tilman, & Oakley, 2009; Cadotte & Davies, 2016). Therefore, we computed not only species diversity but also functional and phylogenetic diversity and performed trait-based analyses to compare the ecological function and conservation value of secondary grasslands on river embankments and seminatural grasslands. We hypothesized that the secondary grasslands of river embankments have the potential to act as refuges for many plant species and provide important ecological functions that play a crucial role in sustaining the functionality of ecosystems within agricultural landscapes.

2 | MATERIAL AND METHODS

2.1 | Study area and sampling

The study sites were located in the eastern part of the Great Hungarian Plain, in the proximity of the Körös and Maros Rivers (Figure 1). The climate of this region is moderately warm and dry. The mean annual temperature is 10.2–10.6°C, and the mean annual precipitation is 500–550 mm. The main soil types within the study area are chernozem, alluvial and meadow soils (Dövényi, 2010).

Both the Körös and Maros Rivers flow in a westerly direction and are among the major rivers of the Great Hungarian Plain. The hydrograph of the larger rivers in this landscape usually shows two floods: snowmelt-induced floods occur in early spring and rain-induced floods in early summer (Bátori et al., 2016). We chose a 100-km-long section of the Körös River and a 40-km-long section of the Maros River for vegetation sampling. The embankments along these rivers were established in the 18th and 19th centuries to prevent the adverse effects of flood and to provide land for agriculture (Bátori et al., 2016). The slopes of embankments were sown with seed mixtures of native grasses (e.g., *Arrhenatherum elatius*, *Alopecurus pratensis*, *Bromus inermis* and *Lolium perenne*) in order to reduce erosion and to produce fodder for livestock. At that time, natural grasslands were widespread in the vicinity of the rivers, and soils originating from these grasslands were also used for the construction of the embankments. The current crest width of embankments usually ranges between 4 and 6 m, their height is about 4.5 m, while the ratio for vertical and horizontal dimension of the slopes is 1:3 or 1:4. Soil organic matter content is higher on riverside slopes than landside slopes.

Our previous study indicated that the vegetation on the north-facing landside slopes of the embankments (hereafter "secondary dry grasslands") is similar to the loess grasslands (hereafter "seminatural dry grasslands"), whereas the vegetation on the north-facing riverside slopes of the embankments (hereafter "secondary wet grasslands") is similar to the mesotrophic wet meadows (hereafter "seminatural wet grasslands"). Seminatural dry grasslands in the studied region are dominated by *Festuca rupicola*, but other grasses such as *Agropyron cristatum*, *B. inermis*, *Elymus hispidus* and *Stipa capillata* are also common. The high cover of dicots (e.g., *Fragaria viridis*, *Galium verum*, *Inula germanica*, *Salvia nemorosa* and *Thalictrum minus*) is also typical

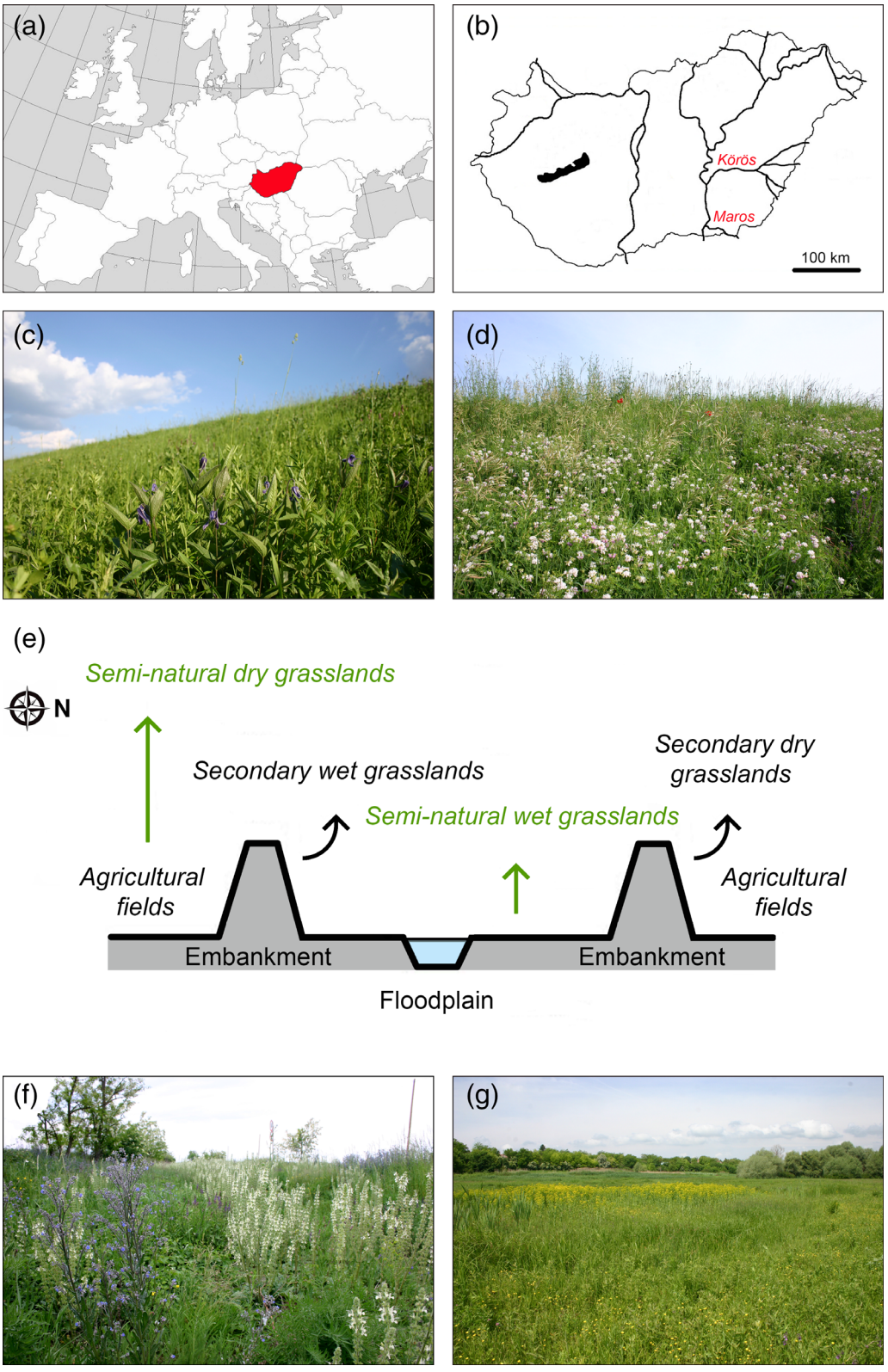

FIGURE 1 Location of the study area in (a) Europe and (b) Hungary; (c) secondary wet grassland on a river embankment; (d) secondary dry grassland on a river embankment; (e) position of the different grassland habitats in the landscape; (f) seminatural dry grassland (i.e., loess grassland) fragments between agricultural fields; (g) seminatural wet grasslands in the floodplain

(Borhidi, Kevey, & Lendvai, 2012). These grasslands have a high conservation value due to their unique species pool. They also provide habitats for several endangered plant species such as *Adonis volgensis*, *Ajuga laxmannii*, *Cynoglottis barrelieri* and *Phlomoides tuberosa*. The dominant species of the seminatural wet grasslands are *A. pratensis*, *Poa pratensis* s.l., and *Poa trivialis*. Many other wet meadow species

are also abundant in this habitat type, including *Carex melanostachya*, *Euphorbia lucida*, *Inula britannica*, *Iris pseudacorus*, *Ranunculus repens*, *Thalictrum lucidum* and *Viola pumila* (Borhidi et al., 2012). Grasslands on embankments are usually managed by machine mowing twice per year, whereas seminatural grasslands have been managed for centuries by various management practices (e.g., mowing and grazing).

In order to obtain representative samples from the study sites, we applied a stratified random sampling approach. The embankments of both rivers were divided into 10 subsections, and both the secondary dry and wet grasslands on the upper two-thirds of embankments were sampled (the lower third was omitted to reduce the effects of periodic floods and therefore habitat heterogeneity) in each subsection using three randomly placed 2 m × 2 m plots in both habitat types (120 plots in total). The age of these grasslands is about 45 years. For comparison, we selected 20 seminatural dry and 20 seminatural wet grassland patches within the study area. We randomly placed three 2 m × 2 m plots in each patch (also 120 plots in total). The percentage cover of each vascular plant species was estimated in May to early June 2017 in all 240 plots (see Supporting Information Table S1). Nomenclature follows The Plant List (http://www.theplantlist.org).

2.2 | Data analysis

To evaluate the ecological functions and conservation value of secondary grasslands on river embankments, we compared them with the seminatural grasslands using the following metrics: species diversity, diagnostic species, phylogenetic diversity, functional diversity and functional trait distributions.

We calculated the Shannon diversity for each plot and the phi (Φ) coefficient of association (Chytrý, Tichý, Holt, & Botta-Dukát, 2002) between species and habitat (i.e., secondary dry grasslands vs. seminatural dry grasslands and secondary wet grasslands vs. seminatural wet grasslands). We considered a species diagnostic if it had 0.2 or higher phi value in a particular grassland type (Fisher exact test; $p < .01$). If a species proved to be diagnostic for more than one grassland type, it was considered diagnostic species to the grassland in which it had a higher phi value. For the further evaluation of these diagnostic species, we classified them into three groups based on their habitat preferences (Borhidi, 1995). The three groups were (a) dry grassland specialists, (b) wet grassland specialists and (c) generalist species (i.e., cosmopolitan species, weeds and nonindigenous species).

For the analysis of phylogenetic diversity, phylogenetic trees were created based on a dated, ultrametric phylogenetic tree of European plants (Durka & Michalski, 2012) and the genera occurring in the studied habitats. The cover values of species from the same genus were summarized. Polytomies were retained as they were represented in the original tree. Phylogenetic diversity of the grasslands was compared using the mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) indices. MPD calculates the MPDs among different taxa, whereas MNTD calculates the mean phylogenetic distance to the closest relative for particular taxa. These two indices capture different aspects of phylogenetic diversity. MPD is generally thought to be more sensitive to tree-wide patterns of phylogenetic diversity, whereas MNTD is more sensitive to the patterns of the tips of the phylogeny (Kembel et al., 2010). These two indices are suitable measures of phylogenetic diversity and are less confounded by species richness than other phylogenetic diversity indices. Therefore, they are appropriate measures in studies where species diversity was also calculated (Barak et al., 2017).

As a measure of functional diversity, we calculated plot-level Rao's quadratic entropy using leaf-height-seed traits (specific leaf area [SLA], plant height and seed mass), flowering traits (flowering period, starting time of flowering and pollination type) and persistence traits (life-form, growth form and lateral spread; Botta-Dukát, 2005; Weiher et al., 1999; Westoby, 1998). Plot-level community-weighted means (CWMs) of single traits were calculated for four traits: SLA, plant height, seed mass and flowering period. The number of insect pollinated plants was calculated for each plot. For the detailed description of the categories and sources of the studied traits, see Table 1.

For the comparisons of diversity indices, CWMs and the number of insect pollinated plants (dependent variables) across seminatural and secondary grassland types, general or generalized linear mixed-effect models with Gamma, Gaussian or Poisson family were used. We applied separate models to compare the dry (secondary dry grasslands vs. seminatural dry grasslands) and wet (secondary wet grasslands vs. seminatural wet grasslands) grassland types. We set sampling location (i.e., subsection) as random factor in the models. Seed mass and flowering period traits were log-transformed.

The calculations of phi values were conducted with the JUICE 7.0.25 programme (Tichý, 2002). Diversity indices and linear models were computed in R environment (R Core Team, 2018). Shannon diversity values were calculated with the "diversity" function of the vegan package (Oksanen et al., 2019). We used the "cophenetic," "ses.mpd" and "ses.mntd" functions of the picante package to calculate phylogenetic diversity (Kembel et al., 2010). Rao's quadratic entropy was calculated with the "dbFD" function of the FD package (Laliberté, Legendre, & Shipley, 2014). The linear mixed-effect models were prepared with the "lme" function of the nlme package (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017) and the generalized liner mixed effect models with the "glmer" function of the lme4 package (Bates, Maechler, & Bolker, 2013).

3 | RESULTS

Both habitat types on embankments (i.e., secondary dry and wet grasslands) showed significantly higher Shannon diversity than their seminatural counterparts (seminatural dry and wet grasslands, respectively; Table 2 and Figure 2). The number of diagnostic species was also higher on the embankments (Table S2): secondary dry grasslands had 25 (e.g., *Bromus hordeaceus*, *Buglossoides arvensis* and *Vicia hirsuta*) and secondary wet grasslands had 29 species (e.g., *Clematis integrifolia*, *P. pratensis* s.l. and *Veronica polita*), whereas seminatural

TABLE 1 Details of the nine traits used for the functional diversity analysis

Trait groups	Trait	Data type	Source
Leaf-height-seed traits	Specific leaf area	Numeric (mm^2/mg)	Kleyer et al. (2008)
	Plant height	Numeric (cm)	Király (2009)
	Seed mass	Numeric (g)	Török et al. (2013, 2016)
Flowering traits	Flowering period	Numeric (months)	Király (2009)
	Starting time of flowering	Nominal with three levels: blooming from early spring (Months 1 to 4); blooming from early summer (Months 5 and 6); blooming from late summer (Months 7 to 9)	Király (2009)
	Pollination type	Nominal with four levels: insect pollination, wind pollination, self-pollination and insect and self-pollination	Kühn, Durka & Klotz (2004)
Persistence traits	Life from	Nominal with six levels: annual monocots, annual dicots, perennial monocots, perennial dicots, small shrubs and trees and shrubs	Király (2009)
	Growth form	Nominal with seven levels: tall erect forbs without rosette or semirosette; tall erect forbs with rosette or semirosette; short, crawling forbs without rosette or semirosette; short, crawling forbs with rosette or semirosette; nontussock forming graminoids; tussock forming graminoids and woody species	Király (2009)
	Lateral spread	Ordinal with three values: <1 cm/year; between 1 and 25 cm/year; >25 cm/year	Klimešová & de Bello (2009) and Klimešová, Danihelka, Chrtek, de Bello & Herben (2017)

TABLE 2 Comparisons of secondary grasslands on river embankments and seminatural grasslands (secondary dry grasslands vs. seminatural dry grasslands and secondary wet grasslands vs. seminatural wet grasslands) based on different diversity indices

	Shannon (H)		Rao's quadratic entropy		MPD		MNTD	
	t	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Secondary dry grasslands versus seminatural dry grasslands	−2.02	.050*	−1.56	.128	0.44	.668	3.13	.003*
Secondary wet grasslands versus seminatural wet grasslands	−5.89	<.001*	0.14	.892	0.25	.802	2.85	.007*

Abbreviations: MPD, mean pairwise taxon distance; MNTD, mean nearest taxon distance.
*$p \leq .05$.

dry grasslands had only 12 (e.g., *C. barrelieri*, *S. capillata* and *Verbascum phoeniceum*) and seminatural wet grasslands had 15 diagnostic species (e.g., *Cerastium dubium*, *I. britannica* and *Phalaris arundinacea*).

Although the number of diagnostic species was higher in the secondary grasslands, the proportion of habitat-specific diagnostic species was higher in the seminatural grasslands. The proportion of dry grassland specialists was 20% in the secondary dry grasslands and 75% in the seminatural dry grasslands. Conversely, the proportion of generalist species was 76% in the secondary dry grasslands and 25% in the seminatural dry grasslands (Supporting Information Table S2). The proportion of wet grassland specialists was lower in the secondary wet grasslands (29%) than in the seminatural wet grasslands (67%) and secondary wet grasslands had more generalist species (64%) than seminatural wet grasslands (33%).

Secondary grasslands showed similar MPDs compared with the seminatural grasslands. In contrast, the difference was significant for MNTDs; secondary grasslands showed significantly lower MNTDs than seminatural ones (Table 2; Figure 2). There was no difference between the Rao's index for secondary and seminatural grasslands (Table 2). However, the CWMs of SLA were significantly higher in secondary grasslands (Table 3 and Figure 3). There was no difference in the CWMs of plant height between the secondary and seminatural dry grasslands. In contrast, the CWMs of plant height indicated that secondary wet grasslands had potentially higher vegetation than seminatural wet grasslands. We did not find any significant difference for seed mass CWMs. However, the CWMs of the flowering period were significantly higher in the secondary grasslands of embankments in both comparisons (Table 3 and Figure 3). The number of insect pollinated plants was significantly higher ($p < .001$) in the secondary wet grasslands than in the seminatural wet grasslands, but we did not find any significant difference in the case of dry grasslands ($p = .780$).

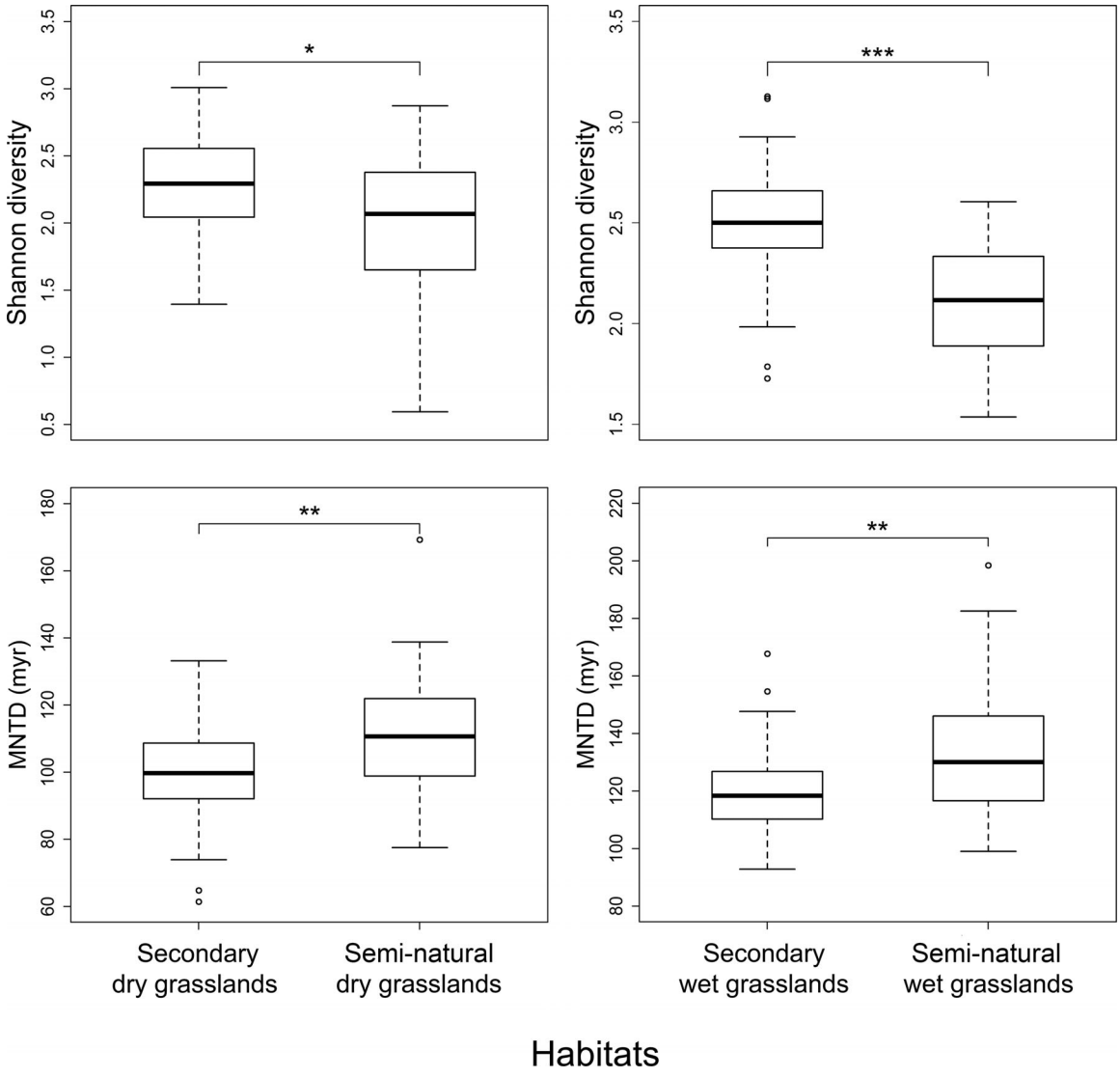

FIGURE 2 Shannon diversity and phylogenetic diversity (MNTD) values for the grassland habitats of embankments and the landscape. Statistically significant differences were marked with asterisks. MNTD, mean nearest taxon distance. *$p < .05$; **$p < .01$; ***$p < .001$

TABLE 3 Comparisons of trait distributions between secondary grasslands on river embankments and seminatural grasslands (secondary dry grasslands vs. seminatural dry grasslands and secondary wet grasslands vs. seminatural wet grasslands)

	Specific leaf area		Plant height		Seed mass		Flowering period	
	t	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Secondary dry grasslands versus seminatural dry grasslands	−3.14	.003*	1.17	.243	−1.52	.137	−3.26	.002*
Secondary wet grasslands versus seminatural wet grasslands	−2.15	.040*	−3.78	<.001*	0.46	.649	−3.55	.001*

*$p < .05$.

4 | DISCUSSION

4.1 | Evaluation of ecological function and conservation value

According to the diagnostic species analyses, generalist species play an especially important role in the grasslands of embankments. Cosmopolitan species, nonindigenous species and weeds could initially colonize these fresh surfaces during the construction of the embankments simultaneously with the sown grasses and other species as founders; therefore, the higher abundances of generalist species on the embankments can be a legacy of this founder effect (Egler, 1954; Grime, 1998). The floodplains of the rivers are densely covered by invasive species and weeds, as the rivers can effectively

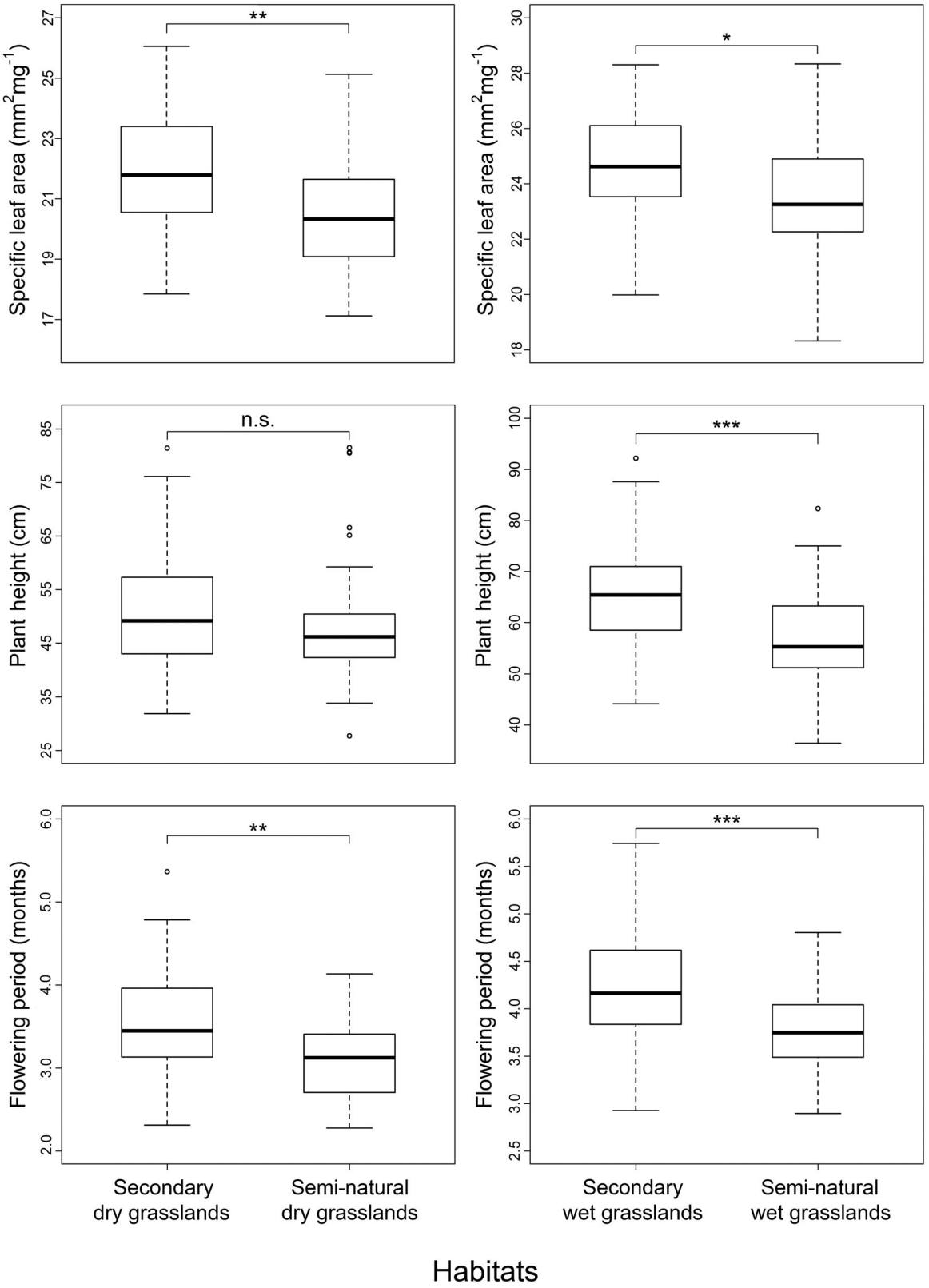

FIGURE 3 Community-weighted means of specific leaf area, plant height and flowering period for the grassland habitats of embankments and the landscape. Statistically significant differences were marked with asterisks. *p < .05; **p < .01; ***p < .001

disperse their propagules to these areas and the disturbance cycle of floods continuously creates new colonization gaps (Bátori et al., 2016). Reconstruction works, dirt roads and the establishment of different flood regulation facilities also create bare surfaces where these species have the potential to colonize successfully once introduced. In addition, the habitats of these embankments are embedded

in the matrix of agricultural land with a high perimeter–area ratio. These circumstances can provide good opportunities for many generalist species to survive on the embankments (cf. Theoharides & Dukes, 2007). Although the high species richness of generalist species significantly increased the Shannon diversity on the embankments; these species did not increase the functional diversity of the grasslands because of their similar functional traits. Therefore, the functional structure of these secondary grasslands is similar to that in the seminatural grasslands of the landscape.

Most studies agree that disturbance has the potential to decrease phylogenetic diversity (Barak et al., 2017; Dinnage, 2009; Turley & Brudvig, 2016). Barak et al. (2017) found that prairies that had been restored using seed sowing had lower phylogenetic diversity compared with natural prairie stands, as the MPD and MNTD of the restored prairies showed significantly more clustered structure than those of the natural ones. Turley and Brudvig (2016) showed that old-fields had significantly lower phylogenetic diversity compared to habitats that had never been cultivated. Similar results were obtained by Helmus et al. (2010), who found that disturbances in lakes resulted in clustering in the phylogenetic structure of the zooplankton community. Based on the theory of environmental filtering and limiting similarity, the phylogenetically clustered structure of the secondary habitats can be expected, as disturbance may weaken the strength of competition (Dinnage, 2009). The MNTD analyses supported this theory, as the values of these indices were lower for the secondary grasslands on embankments than for the seminatural grasslands. It also means that the vulnerability of these secondary grasslands is higher and their resilience is lower against the invasion of alien species (Lososová et al., 2015).

Therefore, our results support the conclusion of recent studies showing that the precise assessment of the ecological function and conservation value of different habitats cannot solely be based on species-based diversity indices, as they are not sensitive to functional redundancy and other functional consequences of species identity (Díaz & Cabido, 2001; Kelemen et al., 2017; Petchey & Gaston, 2006; Schleuter et al., 2010; Tilman et al., 1997). The Shannon diversity indices together with the diagnostic species and the MNTD analyses suggested that the reason for the higher diversity in these secondary grasslands is the higher proportion of generalist species that are functionally and phylogenetically more clustered compared with the species pool of the seminatural grasslands.

Our results on single traits can also help understanding vegetation responses to certain environmental circumstances and potential ecosystem services provided by the vegetation. Species with high SLA can respond rapidly to environmental changes (fast plants) because of their high efficiency of photosynthesis and fast growth (Kelemen et al., 2016; Westoby, 1998). Thus, these species can be more successful on the river embankments where environmental conditions are less stable due to human disturbance and periodic management (mowing twice a year) than in their seminatural counterparts. One of the main ecosystem services of grasslands is hay production. Productivity often correlates positively with plant height, therefore the secondary grasslands on the embankments probably supply higher amount of hay compared with the seminatural grasslands (cf. Bátori et al., 2016). Moreover, the larger mean SLAs in the grasslands on embankments indicate better quality of hay, because grazers prefer species with high nutritional values, which generally positively correlate with SLA (Bullock et al., 2001; Mladek et al., 2013; Moretto & Distel, 1997). The longer flowering period and the presence of more insect pollinated plants in these secondary grasslands are favourable for the pollinator assemblages and also for the palynivores. This ecosystem service can support the maintenance of insect diversity, and can be beneficial for insect pollinated crop plants.

4.2 | Implications for conservation

Both the landside and riverside slopes of the embankments of the Körös and Maros Rivers may provide important habitats for the preservation of both dry and wet grassland species in the future. Embankments play a key role in the prevention of flooding of agricultural fields, therefore the continuous grassland cover is assured on them (i.e., the risk of ploughing and afforestation is negligible), which has important implications for the planning of landscape-scale restoration strategies. Grassland restoration on river embankments can be a sustainable option in the long term, as water management authorities aim to manage and maintain permanent grasslands. It would be advisable to allocate resources for the restoration of grasslands on embankments in restoration planning, as they can be considered temporally stable refuges. To ensure the increase of the conservation value of these grasslands, their management should be better coordinated. For instance, mowing at the same time of each year may be unfavourable for both plants and animals. Instead, temporally and spatially variable management practices (e.g., mowing and/or light grazing) are recommended (Sallai et al., 2011; Vadász, Máté, Kun, & Vadász-Besnyői,-2016; Valkó, Török, Matus, & Tóthmérész, 2012) to ensure the reproduction of most plant species in the long run (Moinardeau, Mesléard, Ramone, & Dutoit, 2019) and to prevent the critical decrease of biomass, which is also important for the protection against erosion.

The embankments of the investigated rivers are situated in agricultural landscapes; therefore, the colonization potential of many grassland specialist species (i.e., dry grassland and wet grassland species) is limited. Consequently, active restoration would be needed to ensure the establishment of these species on the embankments. To increase the number and abundance of valuable dry and wet grassland species in the grasslands of the embankments, hay transfer from seminatural habitats and sowing of regional seed mixtures would provide feasible solutions (Klimkowska et al., 2010; Török et al., 2010).

Secondary grasslands on river embankments have the potential to act as refuge sites for many plant species and may provide important ecological functions in the future. Proper management practices are needed to improve the quality of these secondary habitats.

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DATA AVAILABILITY STATEMENT

The authors confirm that the data supporting the findings of this study are available within the article [and/or] its supplementary materials.

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REFERENCES

Baessler, C., & Klotz, S. (2006). Effects of changes in agricultural land-use on landscape structure and arable weed vegetation over the last 50 years. *Agriculture, Ecosystems & Environment*, *115*, 43–50. https://doi.org/10.1016/j.agee.2005.12.007

Barak, R., Williams, E. W., Hipp, A. L., Bowles, M. L., Carr, G. M., Sherman, R., & Larkin, D. J. (2017). Restored tallgrass prairies have reduced phylogenetic diversity compared with remnants. *Journal of Applied Ecology*, *54*, 1080–1090. https://doi.org/10.1111/1365-2664.12881

Bastian, O., & Bernhardt, A. (1993). Anthropogenic landscape changes in Central Europe and the role of bioindication. *Landscape Ecology*, *8*, 139–151.

Bates, D., Maechler, M., & Bolker, B. (2013). *lme4: Linear mixed-effects models using S4 classes*. R Package Version 0.999999–2. Retrieved from http://cran.r-project.org/package=lme4

Bátori, Z., Körmöczi, L., Zalatnai, M., Erdős, L., Ódor, P., Tölgyesi, C. S., … Török, P. (2016). River dikes in agricultural landscapes: The importance of secondary habitats in maintaining landscape-scale diversity. *Wetlands*, *36*, 251–264. https://doi.org/10.1007/s13157-016-0734-y

Bátori, Z., Vojtkó, A., Keppel, G., Tölgyesi, C. S., Čarni, A., Zorn, M., … Breg Valjavec, M. (2020). Anthropogenic disturbances alter the conservation value of karst dolines. *Biodiversity and Conservation*, *29*, 503–525. https://doi.org/10.1007/s10531-019-01896-4

Benton, G. T., Vickery, A. J., & Wilson, D. J. (2003). Farmland biodiversity: Is habitat heterogeneity the key? *Trends in Ecology & Evolution*, *18*, 182–188.

Biró, M., Bölöni, J., & Molnár, Z. (2018). Use of long-term data to evaluate loss and endangerment status of Natura 2000 habitats and effects of protected areas. *Conservation Biology*, *3*, 660–671. https://doi.org/10.1111/cobi.13038

Borhidi, A. (1995). Social behaviour types, the naturalness and relative ecological indicator values of the higher plants in the Hungarian flora. *Acta Botanica Hungarica*, *39*, 97–181.

Borhidi, A., Kevey, B., & Lendvai, G. (2012). *Plant communities of Hungary*. Budapest: Akadémiai Kiadó.

Botta-Dukát, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, *16*, 533–540. https://doi.org/10.1111/j.1654-1103.2005.tb02393.x

Bullock, J. M., Franklin, J., Stevenson, M. J., Silvertown, J., Coulson, S. J., Gregory, S. J., & Tofts, R. (2001). A plant trait analysis of responses to grazing in a long-term experiment. *Journal of Applied Ecology*, *38*, 253–267. https://doi.org/10.1046/j.1365-2664.2001.00599.x

Cadotte, M. C., & Davies, T. J. (Eds.). (2016). *Phylogenies in ecology: A guide to concepts and methods*. Princeton, NJ: Princeton University Press.

Cadotte, M. W., Cavender-Bares, J., Tilman, D., & Oakley, T. H. (2009). Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS One*, *4*, e5695. https://doi.org/10.1371/journal.pone.0005695

Chytrý, M., Tichý, L., Holt, J., & Botta-Dukát, Z. (2002). Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation Science*, *13*, 79–90. https://doi.org/10.1111/j.1654-1103.2002.tb02025.x

Corbit, M., Marks, P. L., & Gardescu, S. (1999). Hedgerows as habitat corridors for forest herbs in Central New York, USA. *Journal of Ecology*, *87*, 220–232. https://doi.org/10.1046/j.1365-2745.1999.00339.x

Core Team, R. (2018). *R: A language and environment for statistical computing*. Vienna, Austria. Retrieved from: R Foundation for Statistical Computing. https://www.R-project.org/

Deák, B., Tóthmérész, B., Valkó, O., Sudnik-Wójcikowska, B., Moysiyenko, I. I., Bragina, T., … Török, P. (2016). Cultural monuments and nature conservation: A review of the role of kurgans in the conservation and restoration of steppe vegetation. *Biodiversity and Conservation*, *25*, 2473–2490. https://doi.org/10.1007/s10531-016-1081-2

Deák, B., Valkó, O., Török, P., Kelemen, A., Bede, Á., Csathó, A. I., & Tóthmérész, B. (2018). Landscape and habitat filters jointly drive richness and abundance of specialist plants in terrestrial habitat islands. *Landscape Ecology*, *33*, 1117–1132. https://doi.org/10.1007/s10980-018-0660-x

Díaz, S., & Cabido, M. (2001). Vive la difference: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, *16*, 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2

Dinnage, R. (2009). Disturbance alters the phylogenetic composition and structure of plant communities in an old field system. *PLoS One*, *4*, e7071. https://doi.org/10.1371/journal.pone.0007071

Dövényi, Z. (Ed.). (2010). *Magyarország kistájainak katasztere [Inventory of microregions in Hungary]*. Budapest: MTA Földrajztudományi Kutatóintézet.

Durka, W., & Michalski, G. S. (2012). Daphne: A dated phylogeny of a large European flora for phylogenetically informed ecological analyses. *Ecology*, *93*, 2297–2297. https://doi.org/10.1890/12-0743.1

Egler, F. E. (1954). Vegetation science concepts. 1. Initial floristic composition, a factor in old-field vegetation development. *Vegetatio*, *4*, 41–417.

Erdős, L., Ambarli, D., Anenkhonov, O., Bátori, Z., Cserhalmi, D., Kiss, M., … Török, P. (2018). The edge of two worlds: A new review and synthesis on Eurasian forest-steppes. *Applied Vegetation Science*, *21*, 345–362. https://doi.org/10.1111/avsc.12382

Fekete, R., Mesterházy, A., Valkó, O., & Molnár, V. A. (2018). A hitchhiker from the beach: The spread of the maritime halophyte *Cochlearia danica* along salted continental roads. *Preslia*, *90*, 23–37.

Fekete, R., Nagy, T., Bódis, J., Biró, É., Löki, V., Süveges, K., … Molnár, V. A. (2017). Roadside verges as habitats for endangered lizard-orchids (*Himantoglossum* spp.): Ecological traps or refuges? *Science of the Total Environment*, *607-608*, 1001–1008. https://doi.org/10.1016/j.scitotenv.2017.07.037

Francis, R. A., Chadwick, M. A., & Turbelin, A. J. (2019). An overview of non-native species invasions in urban river corridors. *River Research and Applications*, *35*, 1269–1278. https://doi.org/10.1002/rra.3513

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, *86*, 902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Helmus, M. R., Keller, W., Paterson, M. J., Yan, N. D., Cannon, C. H., & Rusak, J. A. (2010). Communities contain closely related species during ecosystem disturbance. *Ecology Letters*, *13*, 162–174.

Hobbs, R. J., Higgs, E., & Harris, J. A. (2009). Novel ecosystems: Implications for conservation and restoration. *Trends in Ecology & Evolution*, *24*, 599–605. https://doi.org/10.1016/j.tree.2009.05.012

Kelemen, A., Tóthmérész, B., Valkó, O., Miglécz, T., Deák, B., & Török, P. (2017). New aspects of grassland recovery in old-fields revealed by trait-based analyses of perennial-crop-mediated succession. *Ecology and Evolution*, *7*, 2432–2440. https://doi.org/10.1002/ece3.2869

Kelemen, A., Valkó, O., Kröel-Dulay, G., Deák, B., Török, P., Tóth, K., … Tóthmérész, B. (2016). The invasion of common milkweed (*Asclepias syriaca* L.) in sandy old-fields—Is it a threat to the native flora? *Applied Vegetation Science*, *19*, 218–224. https://doi.org/10.1111/avsc.12225

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., … Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, *26*, 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Király, G. (Ed.). (2009). *Új magyar füvészkönyv. Magyarország hajtásos növényei. Határozókulcsok [New Hungarian Herbal. The Vascular Plants of Hungary. Identification key]*. Jósvafő: Aggteleki Nemzeti Park Igazgatóság.

Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., … Peco, B. (2008). The Leda Traitbase: A database of life-history traits of northwest European flora. *Journal of Ecology*, *96*, 1266–1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x

Klimešová, J., Danihelka, J., Chrtek, J., de Bello, F., & Herben, T. (2017). CLO-PLA: A database of clonal and bud bank traits of central European flora. *Ecology*, *98*, 1179. https://doi.org/10.1002/ecy.1745

Klimešová, J., & de Bello, F. (2009). CLO-PLA: The database of clonal and bud bank traits of central European flora. *Journal of Vegetation Science*, *20*, 511–516. https://doi.org/10.1111/j.1654-1103.2009.01050.x

Klimkowska, A., Kotowski, W., Van Diggelen, R., Grootjans, A. P., Dzierża, P., & Brzezińska, K. (2010). Vegetation re-development after fen meadow restoration by topsoil removal and hay transfer. *Restoration Ecology*, *18*, 924–933.

Kühn, I., Durka, W., & Klotz, S. (2004). BiolFlor—A new plant-trait database as a tool for plant invasion ecology. *Diversity and Distributions*, *10*, 363–365.

Laliberté, E., Legendre, P., & Shipley, B. (2014). *FD: Measuring functional diversity from multiple traits, and other tools for functional ecology*. R Package Version 1.0–12. Retrieved from https://cran.r-project.org/web/packages/FD/index.html

Láníková, D., & Lososová, Z. (2009). Rocks and walls: Natural versus secondary habitats. *Folia Geobotanica*, *44*, 263–280.

Le Viol, I., Mocq, J., Julliard, R., & Kerbiriou, C. (2009). The contribution of motorway stormwater retention ponds to the biodiversity of aquatic macroinvertebrates. *Biological Conservation*, *142*, 3163–3171. https://doi.org/10.1016/j.biocon.2009.08.018

Liebrand, C. I. J. M., & Sykora, K. V. (1996). Restoration of semi-natural, species-rich grasslands on river dikes after reconstruction. *Ecological Engineering*, *7*, 315–326.

Löki, V., Deák, B., Lukács, B. A., & Molnár, V. A. (2019). Biodiversity potential of burial places—A review on the flora and fauna of cemeteries and churchyards. *Global Ecology and Conservation*, *18*, e00614. https://doi.org/10.1016/j.gecco.2019.e00614

Lososová, Z., de Bello, F., Chytrý, M., Kühn, I., Pyšek, P., Sádlo, J., … Zelený, D. (2015). Alien plants invade more phylogenetically clustered community types and cause even stronger clustering. *Global Ecology and Biogeography*, *24*, 786–794. https://doi.org/10.1111/geb.12317

Maltby, E., & Blackwell, M. S. A. (2005). Managing riverine environments in the context of new water policy in Europe. *International Journal of River Basin Management*, *3*, 133–141. https://doi.org/10.1080/15715124.2005.9635253

Mladek, J., Mládková, P., Hejcmanová, P., Dvorský, M., Pavlu, V., de Bello, F., … Pakeman, R. (2013). Plant trait assembly affects superiority of Grazer's foraging strategies in species-rich grasslands. *PLoS One*, *8*, e69800. https://doi.org/10.1371/journal.pone.0069800

Moinardeau, C., Mesléard, F., Ramone, H., & Dutoit, T. (2019). Short-term effects on diversity and biomass on grasslands from artificial dykes under grazing and mowing treatments. *Environmental Conservation*, *46*, 132–139. https://doi.org/10.1017/S0376892918000346

Molnár, V. A., Nagy, T., Löki, V., Süveges, K., Takács, A., Bódis, J., & Tökölyi, J. (2017). Turkish graveyards as refuges for orchids against tuber harvest. *Ecology and Evolution*, *7*, 11257–11264. https://doi.org/10.1002/ece3.3562

Molnár, Z., Biró, M., Bartha, S., & Fekete, G. (2012). Past trends, present state and future prospects of Hungarian forest-steppes. In M. Werger & M. van Staalduinen (Eds.), *Eurasian steppes. Ecological problems and livelihoods in a changing world. Plant and vegetation* (pp. 209–252). Dordrecht: Springer.

Moretto, A. S., & Distel, R. A. (1997). Competitive interactions between palatable and unpalatable grasses native to a temperate semi-arid grassland of Argentina. *Plant Ecology*, *130*, 155–161.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., Minchin, P. R., … Wagner H. (2019). *Vegan: Community ecology package*. R Package Version 2.3–5. Retrieved from http://CRAN.R-project.org/package=vegan

Petchey, O. L., & Gaston, K. J. (2006). Functional diversity: Back to basics and looking forward. *Ecology Letters*, *9*, 741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2017). *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-141. Retreived from https://cran.r-project.org/web/packages/nlme/index.html

Sallai, A., Harcsa, M., Szemán, L., & Percze, A. (2011). Árvízvédelmi földgátak legeltetése és kaszálásos hasznosításának értékelése [The evaluation of the effects of grazing and mowing on river embankments]. *Tájökológiai Lapok*, *9*, 275–284.

Schleuter, D., Daufresne, M., Massol, F., & Argillier, C. (2010). A user's guide to functional diversity indices. *Ecological Monographs*, *80*, 469–484. https://doi.org/10.1890/08-2225.1

Süveges, K., Löki, V., Lovas-Kiss, Á., Ljubka, T., Fekete, R., Takács, A., … Molnár, V. A. (2019). From European priority species to characteristic apophyte: *Epipactis tallosii* (Orchidaceae). *Willdenowia*, *49*, 401–409. https://doi.org/10.3372/wi.49.49310

Theoharides, K. A., & Dukes, J. S. (2007). Plant invasion across space and time: Factors affecting nonindigenous species success during four stages of invasion. *New Phytologist*, *176*, 256–273.

Tichý, L. (2002). JUICE, software for vegetation classification. *Journal of Vegetation Science*, *13*, 451–453. https://doi.org/10.1111/j.1654-1103.2002.tb02069.x

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., & Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, *277*, 1300–1302. https://doi.org/10.1126/science.277.5330.1300

Timmermann, T., Margóczi, K., Takács, G., & Vegelin, K. (2006). Restoration of peat-forming vegetation by rewetting species-poor fen grasslands. *Applied Vegetation Science*, *9*, 241–250. https://doi.org/10.1111/j.1654-109X.2006.tb00673.x

Torma, A., & Császár, P. (2013). Species richness and composition patterns across trophic levels of true bugs (Heteroptera) in the agricultural landscape of the lower reach of the Tisza River basin. *Journal of Insect Conservation*, *17*, 35–51. https://doi.org/10.1007/s10841-012-9484-1

Török, P., Deák, B., Vida, E., Valkó, O., Lengyel, S., & Tóthmérész, B. (2010). Restoring grassland biodiversity: Sowing low-diversity seed mixtures can lead to rapid favourable changes. *Biological Conservation*, *143*, 806–812. https://doi.org/10.1016/j.biocon.2009.12.024

Török, P., Miglécz, T., Valkó, O., Tóth, K., Kelemen, A., Albert, Á., … Tóthmérész, B. (2013). New thousand-seed weight records of the Pannonian flora and their application in analysing social behaviour types. *Acta Botanica Hungarica*, *55*, 429–472. https://doi.org/10.1556/ABot.55.2013.3-4.17

Török, P., Tóth, E., Tóth, K., Valkó, O., Deák, B., Kelbert, B., … Tóthmérész, B. (2016). New measurements of thousand-seed weights of species in the Pannonian flora. *Acta Botanica Hungarica*, *58*, 187–198. https://doi.org/10.1556/034.58.2016.1–2.10

Turley, N. E., & Brudvig, L. A. (2016). Agricultural land-use history causes persistent loss of plant phylogenetic diversity. *Ecology*, *97*, 2240–2247. https://doi.org/10.1002/ecy.1443

Vadász, C., Máté, A., Kun, R., & Vadász-Besnyői, V. (2016). Quantifying the diversifying potential of conservation management systems: An evidence-based conceptual model for managing species-rich grasslands. *Agriculture, Ecosystems & Environment*, *234*, 134–141. https://doi.org/10.1016/j.agee.2016.03.044

Valkó, O., Török, P., Matus, G., & Tóthmérész, B. (2012). Is regular mowing the most appropriate and cost-effective management maintaining diversity and biomass of target forbs in mountain hay meadows? *Flora*, *207*, 303–309. https://doi.org/10.1016/j.flora.2012.02.003

Varga, K., Dévai, G., & Tóthmérész, B. (2013). Land use history of a floodplain area during the last 200 years in the upper-Tisza region (Hungary). *Regional Environmental Change*, *13*, 1109–1118. https://doi.org/10.1007/s10113-013-0424-8

Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E., & Eriksson, O. (1999). Challenging Theophrastus: A common core list of plant traits for functional ecology. *Journal of Vegetation Science*, *10*, 609–620. https://doi.org/10.2307/3237076

Westoby, M. (1998). A leaf–height–seed (LHS) plant ecology strategy scheme. *Plant and Soil*, *199*, 213–227.

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